Fossil protists (algae and testate protozoans) in the marine Phanerozoic of Western Australia: a review through latitudinal change, climate extremes, and breakup of a supercontinent

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Abstract

Algae and testate protozoans in Western Australian Cambrian-Neogene marine deposits are reviewed in terms of their broad occurrence. Known groups include: organic-walled unicellular phytoplankton, mostly algae (acritarchs and dinoflagellates); calcareous unicellular algal phytoplankton (calcareous nannoplankton and calcareous dinoflagellate cysts); benthic calcareous macroalgae as well as the enigmatic *Tubiphytes*; testate protozoans, including Foraminifera and Radiolaria; and groups of uncertain affinity including calcareous tests of Calcitarcha, tuberitinids, Draffania, and possible Charophyta. A record of calpionellids from the uppermost Jurassic of the Canning Basin is discounted. In addition to the groups listed above, stromatolites and calcareous and organic-walled cyanobacteria are considered and chitinozoans are included in this discussion although their biological group affinities are uncertain. The stratigraphic and geographic distribution of these fossil groups depended mainly on: (1) major evolutionary events; (2) latitudinal position from warm low latitudes in the Northern Hemisphere during the Early Paleozoic, to cold ĥigh latitudes in the Southern Hemisphere during the Pennsylvanian and earliest Permian, and later to warmer mid southern latitudes; and (3) the nature of the sedimentary basins and the seas that inundated these regions during phases of breakup of the Gondwana supercontinent. The basins developed within the interior of East Gondwana during the Paleozoic to middle Mesozoic and then along a continental margin newly formed by the progressive north-south opening of the Indian Ocean from the Middle Jurassic to Early Cretaceous. These changes in ocean configuration led to a significant diversification of dinoflagellates, calcareous nannoplankton, and Foraminifera: all of which are important stratigraphic guide fossils in the Jurassic to Cretaceous strata.

Keywords: Paleozoic, Mesozoic, Cenozoic, Acritarchs, Dinoflagellates, Calcareous nannofossils, Macroalgae, Foraminifera, Radiolaria, Western Australia

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INTRODUCTION

Marine deposits of each Phanerozoic system from the Cambrian to the Quaternary are present in sedimentary basins on mainland Western Australia and on the adjacent continental shelf and contiguous deep-water marginal plateaus (Geological Survey of Western Australia 1990). The Paleozoic and early Mesozoic marine record is from basins that were positioned in the interior of East Gondwana (Fig. 1A, C). These shallow-marine basins are confined mainly to the north of the State with a marine influence extending as far south as the central Perth Basin (Jurien area) during some periods. Broadscale climate variation in interior East Gondwana ranged from equatorial warm and dry conditions during the early and middle Paleozoic to high-latitude continental ice cover during part of the Pennsylvanian (Late Carboniferous) followed by alternating cool and warm intervals during the Permian and a warm wet phase

during the Mesozoic (Tables 1–5). The late Mesozoic and Cenozoic marine basins developed on the newly formed margin of the Australian continent (Fig. 1B). Breakup of Gondwana that led to the formation of the Indian Ocean took place progressively from the late Middle Jurassic (ca. 165 Ma) in the Timor Sea region, to Late Jurassic (ca. 155 Ma) in the Argo Abyssal Plain north of Exmouth Plateau, to Early Cretaceous (ca. 136 Ma) in the Perth Abyssal Plain (Metcalfe 2011; Haig & Bandini 2013; Heine & Müller 2005; Gibbons *et al.* 2013). The Southern Ocean started to open along the southern margin of Western Australia during the Late Cretaceous (ca. 83.5 Ma; Williams *et al.* 2011).

A great diversity of fossil protists, including algae and testate protozoans, is known from the marine deposits (Tables 1–5). The published record of algae comprises: (a) organic-walled unicellular phytoplankton including acritarchs, of uncertain affinity but some probably algae, from the Ordovician to Cretaceous (Fig 2A–C), and algal dinoflagellates from the Triassic to Cenozoic (Fig.

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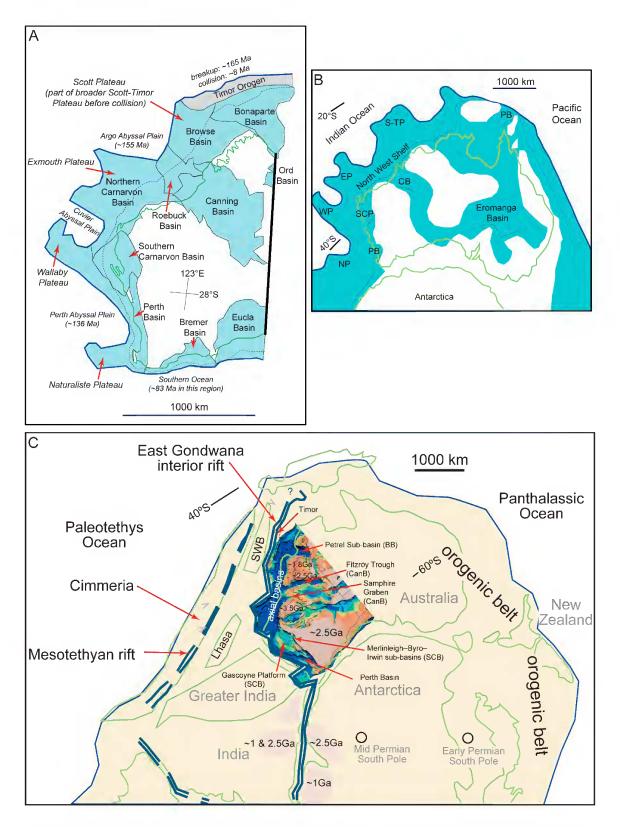


Figure 1. Western Australian Phanerozoic sedimentary basins containing marine strata and examples of past continent configurations. A, Present-day position of basins, shoreline (green line) and the ocean–continent boundary (blue line). The approximate ages of opening of the Indian Ocean and of collision in the Timor region are given in "Ma" units (millions of years before present; see text for references). B, Australian–Antarctic continent reconstruction at about 100 Ma (late Early Cretaceous) and the extent of shallow marine flooding across the continent (blue area; after Henderson *et al.* 2000). C, Reconstruction of East Gondwana at about 290 Ma (Early Permian, Sakmarian), with Western Australia shown by a basement terrane map (compiled by FROGTECH, *www.frogtech.com.au*) with dark blue areas outlining late Paleozoic depocentres (modified from Haig *et al.* 2017).

2G-I); (b) calcareous unicellular algal phytoplankton (calcareous nannoplankton from the Late Triassic to Cenozoic; and calcareous dinoflagellate cysts from the Early Cretaceous); and (c) benthic calcareous macroalgae from the Devonian, Carboniferous, Triassic, and Cenozoic and the enigmatic *Tubiphytes* from the Permian (Fig. 3). The testate protozoans include Foraminifera (Devonian to Cenozoic, Fig. 4) and Radiolaria (Devonian, Cretaceous, Cenozoic). Remane (1971, 1985) disputed Brunnschweiler's (1951, 1960) record of calpionellids from the uppermost Jurassic of the Canning Basin. These small test-like structures require detailed reexamination to establish their true affinities and are not discussed further. In addition to the groups listed above, stromatolites and calcareous and organic-walled cyanobacteria reported from the Phanerozoic of Western Australia are also considered as well as microfossil groups of uncertain affinities from the Devonian and Carboniferous (calcareous tests of Calcitarcha, tuberitinids, Draffania, and possible Charophyta). Because of their small size, simple flask-like morphology and organic-walled test, chitinozoans that are known from the Ordovician and Silurian, are also included in this discussion although their biological group affinities are uncertain.

Different methods are used for the extraction from rock and preparation for study of the algae and testate protozoans (Kummel & Raup 1965). Most of these fossils are minute and large assemblages with many thousands of specimens can be recovered from small rock samples, including core and cuttings from boreholes. Palynomorphs, including the organicwalled cyanobacteria, acritarchs, dinoflagellates and chitinozoans, are usually extracted from mudstone, muddy sandstone, or muddy limestone by digestion in acid, including hydrofluoric acid under highly controlled conditions. The residues are routinely viewed on strew slides under a transmitted-light microscope. Calcareous fossils preserved in limestone including stromatolites, calcareous cyanobacteria, calcareous macroalgae, some of the problematic calcareous algal microfossil groups and calcareous testate protozoans (e.g. many Foraminifera) are studied in thin sections of the rock or in acetate peels, including serial peels, of slabbed limestone surfaces. These are viewed using transmitted-light microscopy. Free specimens of protists with mineralized tests (particularly Foraminifera) are extracted from friable mudstone by disaggregation of the rock and wet sieving, with specimens picked from washed residues using a fine 000 sable-haired brush and mounted onto gridded cardboard microfossil slides. These are routinely viewed under reflected light using a stereomicroscope. Siliceous testate protozoans (radiolarians and organic-cemented siliceous agglutinated Foraminifera) may be extracted from calcareous rocks by digestion of the rock in dilute hydrochloric acid, or from siliceous rocks by digestion, under highly controlled conditions, using dilute hydrofluoric acid. Recently new imaging techniques have become available that are enhancing the description and illustration of the microfossils. These include rendering of multifocal images of three-dimensional microfossils taken under reflected light to produce composite images in sharp focus; micro-CT scanning; and Focused Ion Beam (FIB) imaging.

Stratigraphic ranges of particular species of acritarchs (Ordovician to Triassic) chitinozoans (Ordovician), dinoflagellates (Triassic to Cenozoic), Foraminifera (Late Devonian to Cenozoic) and calcareous nannofossils (Late Triassic to Cenozoic) have great significance in resource exploration in the Western Australian sedimentary basins, particularly for petroleum, water, and geothermal energy exploration. Zonations based on stratigraphic ranges of species are used to define stratigraphic level and age, and for correlation of rock successions within basins, between basins and globally. The distribution patterns of species are compared to modern analogues and used in modelling sedimentary environments in order to build detailed palaeogeographic maps that are used as predictive tools in resource exploration.

This review has three major aims focussed on Western Australian basins. (1) Document the published fossil record of marine algae and testate protozoans from the Cambrian to Neogene. The Quaternary biota is not covered as it is very similar to the modern flora and fauna. (2) Review the significance of selected groups that are particularly important in evolutionary, ecological, or biogeographic studies. (3) Note gaps in the record that may be filled by future study.

SUMMARY OF PUBLISHED RECORD

General background

The presence of marine fossil groups in Western Australian basins is influenced by inter-related factors including: (1) major global geological events; (2) changes in palaeolatitude; (3) changes in climate; (4) changes in local palaeogeography; and (5) marine depositional cycles involving variation in local sea-level caused by tectonic subsidence or uplift and by eustatic (global) sea-level change (Tables 1–5). During Phanerozoic time, Western Australia has been subject to continual change in these factors and this has led to the evolution of our modern fauna and flora.

Knowledge of the fossil groups also depends on the availability of outcrop or of samples from subsurface sections. Much information on groups used for resource exploration remains unpublished either in company proprietary archives or in open-access archives that are now available via the on-line Western Australian Petroleum and Geothermal Information Management System (WAPIMS) of the Geological Survey of Western Australia or the National Offshore Petroleum Information Management System (NOPIMS) of Geoscience Australia. This information is not reviewed here. The published record of algae and testate protozoans is discussed below for five intervals, each summarized on a different table (Tables 1–5).

Early Paleozoic interior seas (20°N-20°S)

Limited successions of marine Cambrian to Silurian strata are available for study in Western Australia (Playford *et al.* 1975; Mory 2017; Table 1). Stromatolites are described only from the Cambrian and organic-walled cyanobacteria, acritarchs, and chitinozoans are known only from subsurface sections of the Ordovician and Silurian. As more borehole sections are cored

Table 1. Summary chart listing key references for protists from Cambrian to Silurian marine strata in Western Australia. Time scale follows Cohen *et al.* (2017); global events follow Gradstein *et al.* (2012); latitudinal range follows Li & Powell (2001); palaeogeography and climate follows Li & Powell (2001) and Mory (2017). Depositional cycles are modified from Trendall & Cockbain (1990). Asterisk after reference indicates species listed but not illustrated.

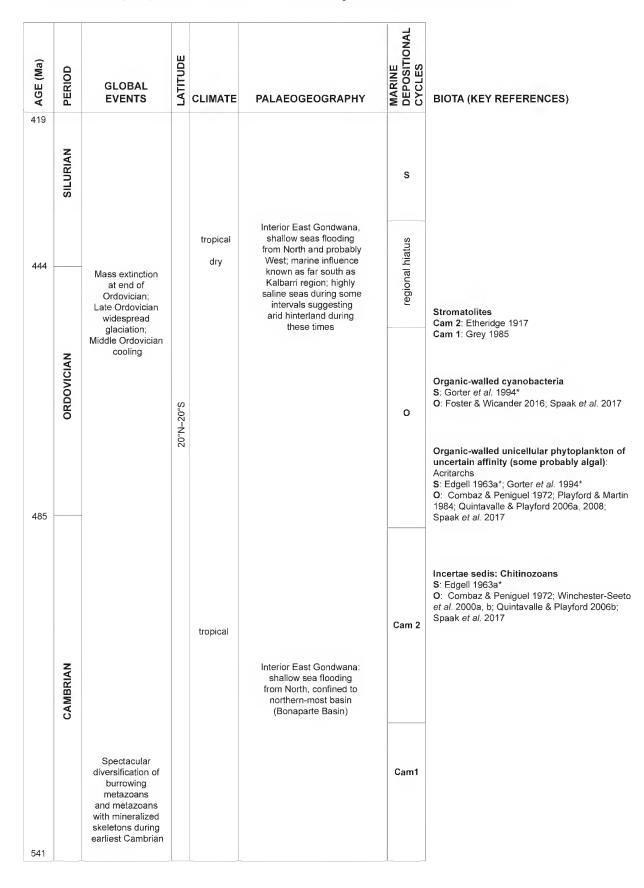


Table 2. Summary chart listing key references for protists from Devonian to Carboniferous marine strata in Western Australia. Time scale follows Cohen *et al.* (2017); global events follow Gradstein *et al.* (2012); latitudinal range follows Li & Powell (2001); palaeogeography and climate follows Li & Powell (2001) and Mory (2017). Depositional cycles are modified from Trendall & Cockbain (1990). Asterisk after reference indicates species listed but not illustrated.

AGE (Ma)	PERIOD and EPOCH	GLOBAL EVENTS	LATITUDE	CLIMATE	PALAEOGEOGRAPHY	MARINE DEPOSITIONAL CYCLES	BIOTA (KEY REFERENCES)
299 323	CARB. (PENNSYLVANIAN)	Global warm spike in latest Pennsylvanian Rapid cooling giving rise to continental ice sheet over much of East Gondwana		Rapid warming leading to melting of ice sheet at ~ 300 Ma Rapid cooling leading to continental ice sheet after ~ 315 Ma	Interior East Gondwana: major hiatus in sedimentation in most basins because of ice- sheet cover; marine deposition continued in northern areas of East Gondwana interior rift system; major rifting during this time led to changes in interior basin configuration		Stromatolites D2: Fenton 1943; Playford & Cockbain1969; Playford et al. 1976; Grey 1982 Benthic calcareous cyanobacteria C1–D2: Mamet & Roux 1983 D2: Wray 1967 Organic-walled unicellular phytoplankton of uncertain affinity (some probably algae) Acritarchs D–C, D2: Playford 1976, 1981; Playford & Dring 1981 Calcareous microalgae (?) of uncertain affinities
359	CARBONIFEROUS (MISSISSIPPIAN)		40°S (late Pennsylvanian)		Interior East Gondwana: shallow seas flooding East Gondwana interior rift system from North and possibly West;	C1	and life mode Calcitarcha C1: Veevers 1970; Mamet & Roux 1983; Vachard <i>et al.</i> 2014 D–C, D2: Wray 1967; Veevers 1970; Mamet & Roux 1983 Tuberitinids C1: Vachard <i>et al.</i> 2014 Incertae sedis <i>Draffania</i> D2: Belford 1967 Benthic calcareous macroalgae (Solenoporaceans,
559		Mass extinction at Frasnian Fammenian boundary (~372 Ma)	0° (Devonian) to 40°S	tropical dry	marine influence known as far south as near Kalbarri; during Mississippian progressively higher salinity conditions were prevalent in very shallow sea in southern region (Southern Carnarvon Basin)		codiaceans, ?dasycladaleans, Bryopsidales; "incertae sedis algae Algospongia" of Vachard <i>et al.</i> 2014) C1 : Veevers 1970; Mamet & Roux 1983; Vachard <i>et al.</i> 2014 D-C, D2 : Wray 1967; Veevers 1970; Riding & Jansa 1976; Mamet & Roux 1983 ? Charophyta C1 : Vachard <i>et al.</i> 2014 D-C, D2 : Edgell 2003 Benthic testate protozoans Foraminifera
	DEVONIAN					D1	C1: Vachard <i>et al.</i> 2014 C1: Vachard <i>et al.</i> 2014 C1, D–C: Marnet & Belford 1968*; Belford 1970 D–C: Edgell 2004 D2: Crespin 1961; Conkin & Conkin 1968; Belford 1970 Radiolaria D2: Nazarov <i>et al.</i> 1982; Nazarov & Ormiston 1983; Aitchison, 1993; Won, 1997a, 1997b
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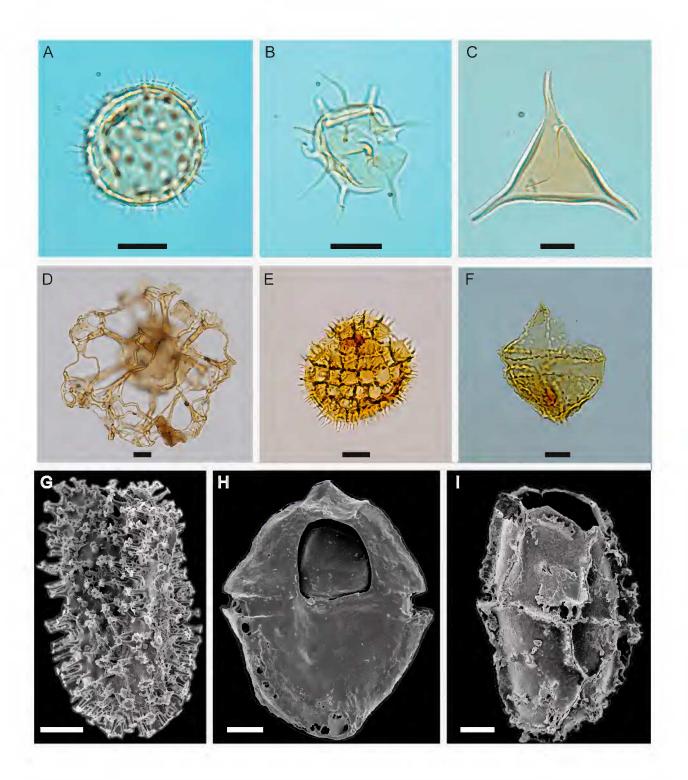


Figure 2. Selected acritarchs and dinoflagellate cysts from Western Australian Basins; A–F, transmitted-light images; G–I, SEM images; bar scales = 10 µm. A–C, acritarchs from the Kockatea Shale, northern Perth Basin, Early Triassic, where they are present in "flood" abundance after the end-of-Permian mass extinction; A, B, *Micrhystridium* spp.; C, *Veryhachium* sp. D–I, dinoflagellate cysts important for biostratigraphic zonation of the Late Triassic and Jurassic; D, *Rigaudella aemula* (Deflandre) Below from the Frigate Formation, Bonaparte Basin (Late Jurassic; Oxfordian); E, *Wanneria listeri* (Stover & Helby) Below from the Brigadier Formation, Northern Carnarvon Basin (Late Triassic; Rhaetian); F, *Rhaetogonyaulax wigginsii* (Stover & Helby) Lentin & Williams from the Mungaroo Formation, Northern Carnarvon Basin (Late Triassic; Carnian–Norian); G, *Prolixosphaeridium capitatum* (Cookson & Eisenack) Singh from the Dingo Claystone, Northern Carnarvon Basin (Late Jurassic; Oxfordian); H, *Scrinodinium crystallinum* (Deflandre) Klement from the Dingo Claystone, Northern Carnarvon Basin (Late Jurassic; Oxfordian); I, *Egmontodinium* sp. from the Dingo Claystone, Northern Carnarvon Basin (Late Jurassic; Oxfordian); I, *Egmontodinium* sp. from the Dingo Claystone, Northern Carnarvon Basin (Late Jurassic; Oxfordian).

through this interval, a greater diversity of algae and testate protozoans may become known. These will add to a significant Australian-wide biogeographic record as East Gondwana drifted from the Northern to Southern Hemisphere. The Western Australian Ordovician acritarch and chitinozoan records are globally important for taxonomic and biogeographic evaluation.

Middle Paleozoic interior seas (0-40°S)

The Canning Basin has an outstanding Middle to Late Devonian carbonate reef-facies succession and similar facies are also present in the Bonaparte Basin (Playford et al. 2009). Limestone sequences extend into the Mississippian (Early Carboniferous) in both basins (Playford et al. 1975; Mory 2017). More environmentally restricted, including hypersaline, carbonate facies of the same age are known in outcrop and in the subsurface in the Southern Carnarvon Basin (Hocking et al. 1987; Mory & Haig 2011). Devonian and Mississippian deposition took place under warm conditions as indicated by the presence of diverse calcareous macroalgae (e.g. Fig. 3A-C), colonial corals, and Foraminifera of the Class Fusulinata (e.g. Fig. 4A-F). During the Pennsylvanian, rapid cooling led to Antarctic-scale continental ice cover across much of Western Australia and adjacent parts of East Gondwana. This is represented by a major regional stratigraphic hiatus overlain by glacially influenced deposits of the latest Pennsylvanian and earliest Permian.

Diverse stromatolites, calcareous cyanobacteria, organic-walled acritarchs, calcareous microalgae (calcitarchans and tuberitinids), calcareous macroalgae, possible charophytes, Foraminifera, and radiolarians are present in the Devonian and Mississippian deposits (Table 2). For global biogeographic comparisons these provide a critical Southern Hemisphere record.

Late Paleozoic East Gondwana interior rift (40-60°S)

An almost complete record of Permian marine deposition is present in Western Australian basins (Hocking *et al.* 1987; Haig *et al.* 2014; Haig *et al.* 2017; Mory 2017) with the biota of the Cisuralian (Early Permian) better known than that of the Guadalupian (Middle Permian) and Lopingian (Late Permian) as indicated on Table 3. In comparison to assemblages known from Permian open continental margins, the Western Australia fossil record is significantly influenced by basin position within a rift system in the interior of a continent, variable climate, and cyclic changes in marine inundation. Because of the different environmental settings, it is difficult to evaluate biogeographic affinities between the Western Australian biota and that from the open peri-Gondwana continental shelf.

The Western Australian basins formed along the axis of the East Gondwana interior rift. This became the site of continental breakup much later during the late Middle Jurassic to the earliest Cretaceous. Marginal rift basins, such as the Petrel Sub-basin (Bonaparte Basin), Fitzroy Trough and Samphire Graben (Canning Basin), and Merlinleigh to Irwin sub-basins (Southern Carnarvon and northern Perth basins) splayed from the axial rift system (Fig. 1A, C). The marginal basins are mudstone dominated, with limestone present only during some of the warm-temperate phases. Within these basins

the rate of deposition almost kept pace with the rate of subsidence and/or eustatic sea-level change. Because of this, low-gradient seafloors and shallow-water depths characterized the inland seas. Depositional cyclicity on various scales is particularly evident in the marginal rift basins where shoaling-upwards shale to sandstone or shale to limestone parasequences form broader scale parasequence sets and sequences. Maximum marine flooding for the entire Permian took place during the late Early Permian (close to the Artinskian-Kungurian boundary). The mudstone-dominated marine successions indicate a humid wet climate in the hinterland as also confirmed by the presence of coal deposits in interbedded fluvial formations. During the earliest Permian, melting of the continental ice sheet led to phases of diamictite (glacial till) deposition. The only other interval of coldwater deposition was during the middle part of the Early Permian (late Artinskian) when sea-ice formed in the southern marginal rift basins, as evidenced by the presence of dropstones in marine mudstone units (Haig et al. 2017). For the remainder of the Permian the climate was temperate with warm-temperate phases during the late Sakmarian (Early Permian), close to the Artinskian–Kungurian boundary in the late Early Permian, late Wordian–Capitanian (Middle Permian), and Wuchiapingian (Late Permian).

The marine Permian of the North West Shelf is related to the Permian of Timor where it occurs in structurally dislocated outcrops (Charlton *et al.* 2002) that are regarded as Gondwanan in origin, and were deposited in the East Gondwana interior rift system contiguous with Western Australian basins (Haig *et al.* 2014, 2017). The warm-temperate phases recognized in the Western Australia basins have equivalent but warmer-water carbonate depositional intervals in Timor. Similar warmwater carbonate deposits are likely to occur in subsurface in the under-explored Permian succession of the northern North West Shelf.

In the Western Australian basins, acritarchs and Foraminifera are generally abundant in marine mudstone facies (Table 3). The Foraminifera are "smaller" benthic types (belonging mainly to organic-cemented agglutinated groups and the calcareous Nodosariata and Miliolata, e.g. Fig. 4G, J, K) whose assemblages change with water depth (Haig 2003). Larger benthic fusulinids are known from limestones in Timor as well as from the Bird's Head region of New Guinea, another area contiguous with the present Australian continent (Haig et al. 2017). The supposed fusulinids reported from the Canning Basin Permian by Chapman & Parr (1937) are not Foraminifera but possibly echinoid spines. Although larger fusulinids are absent, smaller representatives of the Class Fusulinata (e.g. textrataxids, abadehellids, endothyrids and lasiodiscids; e.g. Abadehella sp., Fig. 4H, I) are present in warm-phase limestones in marginalrift and axial-rift basins in Western Australia. Tubiphytes encrustations, of probable algal affinity, are found on skeletal debris in limestones of the late Sakmarian and latest Artinskian-earliest Kungurian warm phases in the marginal rift basins (e.g. Fig. 3D, E).

Mesozoic East Gondwana interior rift (50–30°S)

Triassic to earliest Cretaceous marine sediments deposited before continental breakup in the East **Table 3**. Summary chart listing key references for protists from Permian marine strata in Western Australia. Time scale follows Cohen *et al.* (2017); global events follow Gradstein *et al.* (2012); latitudinal range follows Li & Powell (2001); palaeogeography follows Li & Powell (2001) and Mory (2017). Depositional cycles and climate are modified from Haig & Mory (2016), Haig *et al.* (2017) and unpublished work by Haig and co-authors. Asterisk after reference indicates species listed but not illustrated.

AGE (Ma)	PERIOD and EPOCH	GLOBAL EVENTS	LATITUDE	CLIMATE	PALAEOGEOGRAPHY	MARINE DEPOSITIONAL CYCLES	BIOTA (KEY REFERENCES)
252	LATE PERMIAN (LOPINGIAN)	Most severe mass extinction (> 90% of species) at end of Permian		Temperate humid/wet Warm spike during early Pm5; humid/wet		Pm5	Organic-walled cyanobacteria ?Pm5-2: Segroves 1967 Pm2: Foster <i>et al.</i> 1985 Pm2-Pm1: Foster & Waterhouse 1998* Organic-walled phytoplankton of uncertain affinity (some probably algae) Acritarchs
	MIDDLE PERMIAN (GUADALUPIAN)			Warm spike during mid to late Pm4; humid/wet Temperate humid/wet	Interior East Gondwana:	Pm4	Prm5-2: Segroves 1967 Prm4-1: Backhouse 1991 ?Prm5-?4: Balme & Segroves 1966 Prm2: Foster <i>et al.</i> 1985 Prm2-Prm1: Foster & Waterhouse 1998* Benthic calcareous macroalgae (? affinities) <i>Tubiphyles</i> Prm3: Haig <i>et al.</i> 2017 Prm2: Haig <i>et al.</i> 2014
273	ALIAN)	Progressive opening of Mesotethyan Ocean along the northern margin of Gondwana (separating the Cimmerian block from the rest of East Gondwana)	40-60°S	Temperate humid/wet Warm spike at ~284 Ma; humid/Wet Cold spike during early Pm3	shallow seas flooding East Gondwana interior rift system from North to as far south as central Perth Basin (around Jurien area). Very shallow seas extending into marginal rifts splaying from the axial rift (e.g. Petrel Sub-basin of Bonaparte Basin; Fitzroy Trough and Samphire Graben of Canning Basin; Merlinleigh to Irwin Sub-basins of Southern Carnarvon and northern-most Perth basins). Marginal seas are mainly brackish with normal-marine phases during marine flooding episodes. Maximum marine	Pm3	Benthic testate protozoans Foraminifera Pm5, 3–1: Crespin 1958; Palmieri 1993 Pm3: Parr 1942; Crespin & Belford 1957; Belford 1962, 1968; Haig 2003, 2004, 2018; Haig <i>et al.</i> 2017; Haig & Mory 2016 Pm2: Howchin 1895; Foster <i>et al.</i> 1985; Dixon & Haig 2004; Haig <i>et al.</i> 2014; Taboada <i>et al.</i> 2015*
	EARLY PERMIAN (CISUR			with sea ice Temperate humid/wet in late P2 Warm spike during early	flooding occurred at ~ 284 Ma (within Pm3)	Pm2	
299		Melting of Gondwana ice sheets	1	Pm2; ± dry Cold; waning of ice-sheets		Pm1 – Glacigene	

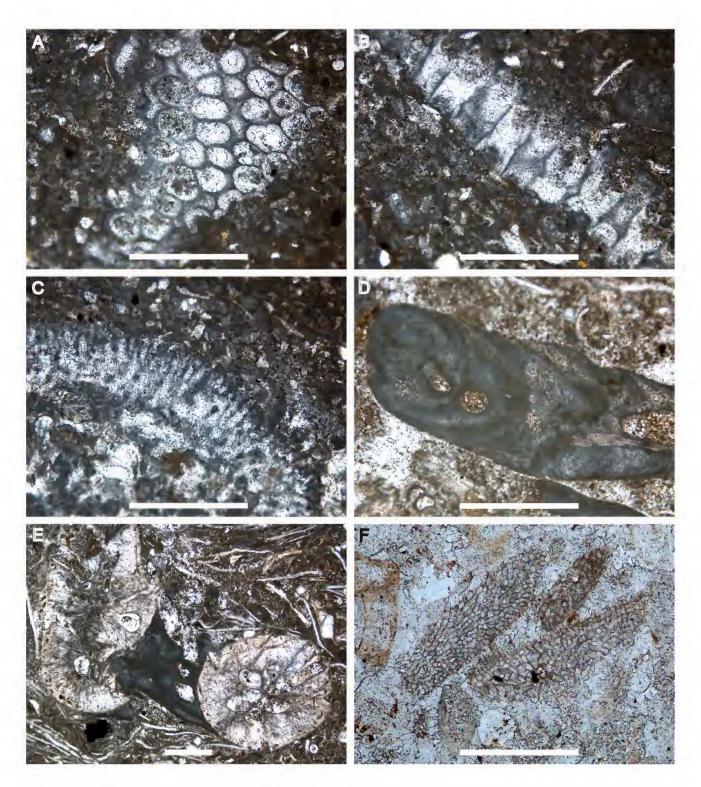


Figure 3. Selected macroalgae and related groups from Western Australian basins; images taken from thin sections viewed in transmitted light (bar scale = 0.5 mm). A, B fragments of probable dasycladalean *Koninckopora tenuiramosa* Wood from the Yindagindy Formation, Southern Carnarvon Basin: A, oblique tangential section across thallus, B, transverse section through portion of thallus; this species is important for confirming the middle Visean (Early Carboniferous) age for this formation. C fragment viewed in slightly oblique transverse section of thallus of the scribroporellacean algae (Order Bryopsidales) *Orthriosiphon*? sp., associated with *K. tenuiramosa* in the Yindagindy Formation. D, fragment of *Tubiphytes* from the lower Callytharra Formation, late Sakmarian (Early Permian) of the Southern Carnarvon Basin, indicative of warm-temperate or warm conditions. E, *Tubiphytes* (central dark area) encrusting two byryozoan skeletons, lower Callytharra Formation of Southern Carnarvon Basin. F, fragments of coralline algae from the Jubilee Member of the Cardabia Calcarenite, Southern Carnarvon Basin, early Eocene; oldest indicators of warm-water conditions in the Western Australian Cenozoic.

Gondwana interior rift system are known mainly in the subsurface of the North West Shelf where an almost continuous marine succession is present. Facies range from very shallow marine to upper bathyal water depths in subsiding rifts. Dinoflagellates (e.g. Fig. 2D–I), acritarchs (Fig. 2A–C), calcareous nannofossils and Foraminifera have been intensely studied in industry exploration work but much of this information is unpublished. The published record is listed on Table 4. Shallow-marine macroalgae and Foraminifera have been described from subsurface cores of Late Triassic limestone indicative of warm-water carbonate platforms. Contiguous Triassic to Early Jurassic sections are exposed in the Timor orogenic belt (Charlton *et al.* 2009; Haig & McCartain, 2010, 2012).

Post-breakup Mesozoic and Cenozoic shelf seas (50–15°S)

The Western Australian continental shelf facing the Indian Ocean developed progressively from north to south during the late Middle Jurassic to earliest Cretaceous. Sandstone and mudstone were deposited in restricted shallow seas on the newly formed shelf, where the outer shelf margin was initially elevated, or in large prograding deltas with high influx of freshwater and sediment. In the ~30 million years following breakup the shelf-margin crust progressively cooled and the margin subsided allowing open-marine shallow-water facies to accumulate. During the Late Cretaceous and Cenozoic chalk or shallow-marine skeletal limestone was deposited over much of the shelf. A few million years after initial breakup large areas of marginal continental crust subsided to lower bathyal water depths (1500-2500 m) forming submarine plateaus contiguous with the continent. These include from north to south (Fig. 1A, B): Scott-Timor Plateau that at about 8 Ma started to collide with the Banda Arc, eventually forming the island of Timor; Exmouth Plateau; Wallaby Plateau; and Naturaliste Plateau.

The Early Cretaceous (Barremian–Albian) seas transgressing across the western continental shelf formed part of a broader marine transgression that covered over 60% of the present Australian mainland (Fig. 1B; Henderson *et al.* 2000). On the Southern Carnarvon Platform, a broad part of the onshore Southern Carnarvon Basin, the deposits of the marginal sea outcrop well and because of this have been the focus of many of the published studies of the testate protozoans of this age.

There is an extensive published record of algal phytoplankton and testate protozoans from outcrop and borehole sections (Table 5). Late Jurassic and Early Cretaceous dinoflagellates (Fig. 2D, G–I) and calcareous nannoplankton are best represented among the algal groups, whereas Cretaceous and Cenozoic benthic and planktonic Foraminifera (Fig. 4L–U) are the best-known testate protozoans. During the transgressive phase of the Aptian–Albian (late Early Cretaceous) marine inundation across the Australian continent (Fig. 1B), radiolarians (siliceous plankton) were preserved in abundance in mudstones of the shelf and interior seas (Haig & Barnbaum 1978; Ellis 1993; Haig 2005). In the Western Australian basins, the microfossil groups record changing water depths and temperatures as continental

crust adjacent the new continental margin cooled and subsided, and the continent slowly drifted north. Benthic foraminiferal assemblages (e.g. Fig. 4L-R) changed from having an estuarine-like interior-sea character during the Barremian-Albian (Early Cretaceous) to more diverse open-marine faunas during the Late Cretaceous (Dixon et al. 2003a,b; Haig et al. 2004). Near the Paleocene-Eocene boundary (ca. 56 Ma) a significant change occurs in the Southern Carnarvon Basin from middle-outer neritic chalk facies, that characterized sea-floor sediment over much of the Southern Carnarvon Platform from the Turonian (Late Cretaceous) to end Paleocene, to middle neritic and shallower limestone facies containing larger benthic Foraminifera (primitive discocyclinids, Fig. 4T; Haig, unpublished observations on the type section of the Jubilee Calcarenite) and coralline macroalgae (Fig. 3F).

SIGNIFICANT PARTS OF RECORD

Organic-walled phytoplankton: cyanobacteria, acritarchs, dinoflagellates

Microscopic, organic-walled phytoplankton groups are present in both marine and freshwater environments. Phytoplankton respond dramatically to external stimuli, especially increased nutrients and temperature (climate change), to form 'algal blooms'; where a litre of water may contain up to a million cells (Davies *et al.* 2016), and the blooms extend over hundreds of kilometres. The fossil record includes globally recognisable bloom events of algae (prasinophytes and dinoflagellates), cyanobacteria and acritarch as described below.

Cyanobacteria

'Blooms' of *Gloeocapsomorpha prisca*, originally described from Middle Ordovician (Darrawillian) and Upper Ordovician organic-rich rocks in Estonia, occur in the Darrawillian upper Goldwyer Formation of the Canning Basin (Spaak *et al.* 2017), and in coeval sediments in Canada: all localities lie within $\pm 10^{\circ}$ N or S of the palaeoequator (Foster *et al.* 1986) and the records reflect growth in optimal shallow warm marine conditions.

Acritarchs

Acritarchs range in size from 5 to ~100 μ m and, by definition, are of unknown affinities although may include «cryptic» dinoflagellates (see *Dinoflagellates*, below). They are common in palynological assemblages recovered from Early Paleozoic rocks, and may show a high diversity of different morphologies, which are attributed to form species. In late Mesozoic acritarch records are rare, and morphologic diversity is low (Playford 2003).

In Western Australia the oldest Phanerozoic acritarchs are known from the Lower Ordovician (late Tremadocian to Floian) Nambeet Formation of the Canning Basin (Combaz & Peniguel 1972; Foster & Wicander 2016). Middle Ordovician acritarch assemblages have been described from the Goldwyer Formation by G. Playford and co-workers (see Table 1 for references). Morphologically, the Nambeet palynoflora is moderately diverse, with shared species known elsewhere from Australia, China, and Canada (Alberta): all localities occur within ±15° S or N of the Early–Middle Ordovician equator (see Foster & Wicander 2016, fig.5), and the assemblage reflects a warm-water marine environment. The Ordovician records illustrate the application of fossil phytoplankton in age determination, and paleoenvironmental/ecological studies. Acritarch assemblages from fully marine conditions show the greatest species (i.e. morphologic) diversity.

Diverse assemblages of acritarchs are documented through the Devonian, particularly the Late Devonian Gneudna Formation of the Carnarvon Basin (Playford 1981; Playford & Dring 1981), and the approximately coeval reef complex at Limestone Billy Hills in the Canning Basin (Colbath 1990). Acritarchs show a marked decline, both quantitatively and qualitatively, in the latest Devonian of the Canning Basin (Playford 1976). As noted above, acritarchs are useful indicators of palaeoenvironmental conditions, often reflecting transgressive and regressive cycles in the sedimentary record (e.g. Wicander & Wood 1997). Molyneaux *et al.* (2013) noted "a high degree of similarity" between acritarch assemblages from the Euramerican region and Australia and China.

Phytoplankton occur in vast numbers, dominating latest Permian-Early Triassic palynofloras from many parts of the world (see Balme 1970). In Western Australia there is an explosion of the acritarch genera Veryhachium and Micrhystridium in assemblages from the basal Kockatea Formation of the Perth Basin (Fig. 2A-C; Haig et al. 2015). The prolific numbers result from a global marine transgressive event which expanded the epicontinental shelf, covering nutrient-rich former exposed land surfaces. Veryhachium first appears in the Lower Ordovician (Tremadocian; Servais et al. 2007) and is recorded through to the Neogene (see Fensome et al. 1990), but there are few periods that show such prolific blooms of this acritarch as the Early Triassic. Following the Early Triassic, acritarchs are much less abundant in younger Mesozoic palynofacies from the Western Australian basins.

Dinoflagellates

Dinoflagellates are single-celled, typically marine, flagellate eukaryotes that are best known in modern environments for creating 'red tides' or algal blooms and their associated shellfish-poisoning events. Many dinoflagellates have both a motile phase and a resting stage where a hypnozygote or thick-walled cyst is formed. These dinoflagellate cysts (typically 15–100 μ m in length) are composed of highly resistant organic polymers (such as dinosporin) and are thus readily preserved, often in large volumes, in fine-grained sedimentary rocks.

Biogeochemical evidence, including the isolation of dinosteranes (steroidal alkanes abundant in extant dinoflagellates) from ancient rocks, and molecular clocks both suggest dinoflagellates originated in the earliest Cambrian or more likely the Neoproterozoic (Moldowan & Talyzina 1998; Fensome *et al.* 1999). However, the oldest unequivocal dinoflagellate cyst (*Sahulidinium ottii*) is not recorded until the Middle Triassic from shallow marine successions in the Bonaparte and Carnarvon basins of northern and north-western Australia (Stover & Helby 1987a). It is also likely that many Paleozoic and Proterozoic acritarchs are 'cryptic' dinoflagellates,

as supported by the strong correlation of dinosteroid abundance and acritarch diversity in pre-Triassic rocks (Moldowan et al. 1996). However, the major Late Triassic radiation of dinoflagellates as they 'switched on' their ability to form fossilized cysts is still considered likely to reflect a real radiative event, rather than just a change in preservation bias (Fensome et al. 1996). This major evolutionary event is well represented in the Carnarvon, Browse and Bonaparte basins as cystforming dinoflagellates likely arose to fill the available marine niches left over from the end Permian mass extinction and abundant new opportunities for rapidly evolving single-celled organisms. The major oil and gas reservoirs hosted in Upper Triassic successions of the Northern Carnarvon Basin have provided ready access to large volumes of samples, thus this first radiation of cyst-forming dinoflagellates is particularly well-studied in the Carnian-Norian marine incursions that are identified throughout the deltaic Mungaroo Formation (Helby et al. 1987; Stover & Helby 1987a; Backhouse & Balme 2002; and numerous unpublished industry reports). Although the species may vary (eg. Hebecysta balmei, Rhaetogonyaulax wigginsii, Fig. 2F, and Wanneria listeri, Fig. 2G, are prominent in Western Australian assemblages), there is notable consistency in the emergence of the key dinoflagellate groups (suessioids and rhaetogonyaulacoids) between the Northern and Southern hemispheres across these stages. For example, the increase in Sverdrupiella in the mid-Norian, best represented in the more open marine conditions of the Bonaparte Basin or outboard Northern Carnarvon Basin, closely mirrors the acmes of this group in the Alaskan and northern Canadian assemblages (Bujak & Fisher 1976). These Arctic dinoflagellate cysts are the only other documented Triassic assemblages of comparable diversity to the western and northern Australian palynofloras. The Rhaetian saw the development of more open marine conditions, and associated carbonate deposition. This is the first interval with an almost complete stratigraphic record of dinoflagellate cysts across the North West Shelf and the often conspicuous presence of Rhaetogonyaulax rhaetica-the first cosmopolitan dinocyst species.

The end-Triassic mass extinction wiped out most dinoflagellate cyst genera with only Dapcodinium and Beaumontella surviving into the Early Jurassic on the North West Shelf. The recovery period was also particularly prolonged, globally, for cyst-forming dinoflagellates compared to other protists. Modest dinoflagellate cyst assemblages do not re-occur until the late Pliensbachian-early Toarcian (late Early Jurassic) Luehndea Assemblage of the Northern Carnarvon and Perth basins. In turn, these are followed by the significant acme of Dissiliodinium caddaense in the earliest Bajocian (early Middle Jurassic); a feature that was first noted in the Cadda Formation of the Perth Basin (Filatoff 1975) and subsequently tracked across most offshore western and northern Australia basins. This event heralded the next major phase of dinoflagellate evolution and morphological diversification through the Bajocian and Bathonian, co-incident with the opening of the Indian Ocean in the northern sector of the Western Australian continental margin. Many of the subsequently dominant dinoflagellate cyst forms first evolved in this period, and the Gonyaulacaceae rose to particular prominence. Various precingular and epicystal archaeopyle types were



Figure 4. Selected Foraminifera from Western Australian basins; B, C, E, F, H-J, T, U, images of sections through foraminifers observed in acetate peels in transmitted light; A, D, images of sections through foraminifers observed in thin sections in transmitted light; G, K, free specimens of foraminifers taken under reflected light; L–S, free specimens of foraminifers taken in SEM. Bar scales = $100 \mu m$. A–F, foraminifers from the Class Fusulinata that evolved in the first major radiation of calcareous species during the Late Devonian and Early Carboniferous (Mississippian). A, Laxoendothyra sp. from lower Fairfield Group, Canning Basin, Upper Devonian (Famennian). B, Endothyra ex. gr. bowmani Phillips from Utting Calcarenite, Bonaparte Basin, Mississippian (middle Visean). C, Plectinopsis michelseni Vachard, Haig and Mory from Yindagindy Formation, Southern Carnarvon Basin, Mississippian (Visean). D, Rectopravina multifida Vachard, Haig and Mory from Yindagindy Formation, Southern Carnarvon Basin, Mississippian (Visean). E, Archaediscus sp. from Utting Calcarenite, Bonaparte Basin, Mississippian (middle Visean). F, Archaediscus sp. from Burvill Formation, Bonaparte Basin, Mississippian (late Visean). G-K, representatives of the main groups of Foraminifera present in the Western Australian Permian. G, organic-cemented siliceous agglutinated Trochammina sp. that is similar to modern T. inflata that inhabits estuarine environments. H, I, off-centered longitudinal and transverse sections through Abadehella sp. (Fusulinata, Abadehellidae), indicative of warm-water conditions, Beekeeper Formation, northern Perth Basin (Guadalupian, Capitanian). J, axial section through porcelaneous Hemigordiopsis sp. from Holmwood Shale, Irwin Subbasin of northern Perth Basin, Early Permian (Cisuralian, Sakmarian). K, lateral view of Pseudonodosaria serocoldensis (Crespin), one of the earliest known Nodosariata with a radiate aperture (visible at top of image), from Noonkanbah Formation, Canning Basin, Early Permian (Cisuralian, close to Artinskian-Kungurian boundary). L-S, representatives of each major foraminiferal group in the Western Australian Cretaceous; L-R are benthic types; S is a planktonic species. L, organic-cemented siliceous agglutinated Ammobaculites humei Nauss from Muderong Shale, Southern Carnarvon Basin, Early Cretaceous (Barremian). M, carbonate-cemented agglutinated Spiroplectinata annectens (Parker & Jones) from upper Gearle Siltstone, Southern Carnarvon Basin, Early Cretaceous (Cenomanian). N, porcelaneous Pseudosigmoilina sp. (Miliolida) from Haycock Marl, Southern Carnarvon Basin, Late Cretaceous (Turonian). O, nodosariid Dentalina delicatula Cushman from Haycock Marl, Southern Carnarvon Basin, Late Cretaceous (Turonian). P, buliminid Turrilina sp. cf. T. evexa (Loeblich & Tappan) from upper Gearle Siltstone, Southern Carnarvon Basin, Late Cretaceous (Cenomanian). Q, Epistomina spinulifera (Reuss) from Gearle Siltstone, Southern Carnarvon Basin, Early Cretaceous (Albian). R, Stensioeina? sp of Howe *et al.* (2000), Haycock Marl, Southern Carnarvon Basin, Late Cretaceous (Turonian). S, *Globotruncana linneiana* (d'Orbigny), Toolonga Calcilutite, Southern Carnarvon Basin, Late Cretaceous (Santonian). T, U, Cenozoic larger benthic Foraminifera (Rotaliida) with complex chamber arrangements viewed in axial sections. T, Discocyclina sp. from the Jubilee Member of the Cardabia Calcarenite, Southern Carnarvon Basin, early Eocene; oldest complex species indicative of warm-water conditions in the Western Australian Cenozoic. U, Lepidocyclina (Nephrolepidina) sp. from the Tulki Limestone, Northern Carnarvon Basin, early Miocene. Discocyclina and Lepidocyclina have similar disc-shaped tests with an equatorial layer overlain on either side by layers of lateral chamberlets. The chamber arrangements in the equatorial layer cannot be seen in the axial sections but differ in these genera.

Table 4. Summary chart listing key references for protists from Mesozoic pre-continental-breakup marine strata in Western Australia. Time scale follows Cohen *et al.* (2017); global events follow Gradstein *et al.* (2012); latitudinal range follows Li & Powell (2001); palaeogeography follows Li & Powell (2001). Depositional cycles are from Marshall & Lang (2013). Asterisk after reference indicates species listed but not illustrated.

AGE (Ma)	PERIOD	GLOBAL EVENTS	LATITUDE	PALAEOGEOGRAPHY	CLIMATE	MARINE DEPOSITIONAL CYCLES	BIOTA (KEY REFERENCES)
132	CRETACEOUS (earliest part)			Final breakup of Australian western margin to form Indian Ocean in Perth area at ~136 Ma		K10	Stromatolites TR10: Lipps & Culver 2002; Chen <i>et al.</i> 2014 Organic-walled algal phytoplankton Dinoflagellates (TR20 and above) ± Acritarchs K10-TR20: Helby <i>et al.</i> 1987; Burger 1996
140	ASSIC	Progressive sea-		Continental breakup to form Indian Ocean in		J50	J50–TR20: Riding <i>et al.</i> 2010 J20: Filatoff 1975; Stover & Helby 1987a; Helby & Stover 1987 Mantle & Riding 2012 TR30–20: Bint & Helby 1988; Brenner 1992a; Brenner & Foster
	LATE JURASSIC	level rise through Jurassic until major fall during latest Jurassic		Argo Abyssal Plain area north of Exmouth Plateau at ~155 Ma Continental breakup to		J40	1994; Backhouse & Balme 2002; Backhouse <i>et al.</i> 2002 TR20: Helby 1987a TR20–10: Stover & Helby 1987a TR10: Medd 1966; Sappal 1978; Haig <i>et al.</i> 2015
164 174	MIDDLE JURASSIC			form Indian Ocean in Timor area at ~165 Ma		J30	Calcareous algai phytoplankton Calcareous nannofossils J50–10: Howe 2000 J20: Shafik 1994 TR30–20: Bralower <i>et al.</i> 1992
	EARLY JURASSIC		30-50°S	Interior East Gondwana: shallow seas flooded East Gondwana interior	Warm	J20	Benthic calcareous macroalgae (codiaceans; dasycladaleans; udoteaceans,) TR30–20: Von Rad <i>et al.</i> 1990; Röhl <i>et al.</i> 1991 Benthic testate protozoans Foraminifera
		Severe mass	30	rift system from North to as far south as central Perth Basin (around	humid/wet	J10	Late Jurassic: Quilty 2011 J20: Bartenstein & Malz 2001 J20-10: Apthorpe 1994*; Quilty 1981a; TR30-20: Quilty 1990; Von Rad <i>et al.</i> 1990;
201		extinction at end of Triassic		Jurien area). Carbonate- platforms including reefs developed on topographic highs in northern parts of axial		TR30	Röhl <i>et al.</i> 1991; Zaninetti <i>et al.</i> 1992; Kristan-Tollmann & Gramann 1992 TR10 : Heath & Apthorpe 1986; Apthorpe 2003; Haig <i>et al.</i> 2015
	LATE TRIASSIC			rift system. Large deltas formed at basin margins and fluvial conditions were present in the southern axial basins. Only during the Early Triassic did very shallow		TR20	
	LATE T			seas flood the marginal rifts splaying from the axial rift system			
237						TR10	
	MIDDLE TRIASSIC						
247 252	щЧ						

Table 5. Summary chart listing key references for protists from late Mesozoic and Cenozoic post-continental-breakup marine strata in Western Australia. Time scale follows Cohen *et al.* (2017); global events follow Gradstein *et al.* (2012); latitudinal range follows Li & Powell (2001); palaeogeography follows Li & Powell (2001). Depositional cycles for the Jurassic and earliest Cretaceous are from Marshall & Lang (2013). SCP numbers indicate marine depositional cycles recognized in the onshore Southern Carnarvon Basin (Haig & Mory 2003; Haig *et al.* 2004; Haig 2005 and unpublished data). Publications on the Southern Carnarvon and northern Perth basins are listed under SCP cycles. Away from these basins, publications are listed under broad age categories (abbreviations: Cen = Cenozoic; Neo = Neogene; Pal = Paleogene; L Cret = Late Cretaceous; E Cret = Early Cretaceous). Asterisk after reference indicates species listed but not illustrated.

AGE (Ma)	PERIOD or EPOCH	GLOBAL EVENTS	LATITUDE	CLIMATE	PALAEOGEOGRAPHY	MARINE DEPOSITIONAL CYCLES	BIOTA (KEY REFERENCES)
2.58		Polar ice sheets from latest Miocene; Cooling from Early to mid-Miocene climatic optimum.	15-35°S	Warm dry	Shallow warm seas flooded Southern Carnarvon Platform and basins along southern continental margin at ~ 17 Ma	SCP12	Organic-walled algal plankton Dinofiagellates (± acritarchs) [cysts] Cen-J30: Cookson & Eisenack 1974, 1982 Pal: Cookson & Eisenack 1967 Cret: Cookson & Eisenack 1970 Cret-J50: Cookson & Eisenack 1958 Cret-J30: Helby et al. 1987; Stover & Helby 1987a; Riding & Helby 2001a-h SCPP-3: Haig et al. 2004* SCP7-4: Cookson & Eisenack 1960a, 1962, 1968
23	OLIGOCENE	Major global cooling during Oligocene		? wet	Formation of extensive laterite, silicrete, and calcrete in soils on land		SCP7-2: Dixon et al. 2003a*,b* E Cret: Eisenack & Cookson 1960; Brenner 1992b SCP4: Deflandre & Cookson 1955; Cookson 1956; Cookson & Eisenack 1962a,b, 1969, 1971; Backhouse 2006 SCP4-SCP1: Backhouse 1987, 1988 SCP2: McLoughlin et al. 1995
	PALEOGENE EOCENE	Complete opening of Southern Ocean by ~45 Ma		Warm dry	Shallow warm seas flooded Southern Carnarvon Platform and basins along southern continental margin at ~	SCP11	SCP1-J50:Cookson & Eisenack 1960b K10: Helby & Stover 1987b; Stevens 1987; Stevens & Helby 19 May <i>et al.</i> 1987 K10-J50: Helby 1987b J50: Stover & Helby 1987b; Bint & Marshall 1994 J30-20: Mantie 2009a,b
	PALEOC.	Paleocene-Eocene Thermal Maximum at ~ 56 Ma			41 Ma Post-rift thermal	SCP10	J30: Mantie 2005 Calcareous algal plankton Calcareous dinoflagellate cysts E. Cret: Keupp 1992 Calcareous nannofossils Neo: Siesser <i>et al.</i> 1992b
66		Severe mass			subsidence and global sea-level rise, led to	SCP9	Neo-Pal: Siessor & Bralower 1992 Neo-L Cret: Shafik 1991
	LATE CRETACEOUS	extinction at end of Cretaceous			extensive areas of open-marine chalk deposition on parts of shelf Until ~95 Ma, the new shelf in the Carnarvon and Perth Basins was flooded by restricted seas with muddy substrates, probably caused by an elevated shelf edge on ocean side. Marine flooding across Australia was out of	SCP8	Pal-L Siesser et al 1992a Pal-L Cret: Pospichal & Bralower 1992 L Cret: Howe et al. 2003; Campbell et al. 2004 Cret: Bralower & Siesser 1992; Shafik 1994 SCP8-3: Shafik 1990; Haig et al. 2004* SCP7-2: Dixon et al. 2003a*,b* SCP7-5: Howe et al. 2000 SCP4: Haig et al. 1996 J50-J30: Howe 2000 Calcareous macroalgae Pal: Cockbain 1969 Testate protozoans Foraminifera (benthic and/or planktonic) Neo: Crespin 1955* Neo-L. Cret: Quilty 1974 Neo-L. Cret: Quilty 1978 SCP12-3: Edgell 1952* Pal: Quilty 1969, 1975, 1981b; McGowran & Lindsay 1969; McGowran 1977*, 1989* SCP11. Chapman & Crespin 1935; Cockbain 1967, 1968, 19' 1978, 1981, Haig et al. 1997, Haig & Mory 2003 SCP10: Parr 1938; Coleman 1950*; McGowran 1964; Haig et al. 2003; Left: Edgell 1964*, McGowran 1977*; Howe et al. 2003;
		Max. sea-levels (>250 higher than present)		Temperate dry in		SCP7	
		Global ocean		southern areas		SCP6	
100		bottom-water anoxia at ~93 Ma				SCP5	
	ACEOUS					SCP4	
	EARLY CRETACEOUS			Cool		SCP3	
				temperate		SCP2	
	ш			humid/wet	step with global sea-level.	SCP1	Campbell <i>et al.</i> 2004; Petrizzo 2000; Petrizzo & Premoli Silva 2000; Petrizzo 2003 L–E Cret.(Alb): Haig 1992; Wonders 1992
145		Major changes in ocean circulation with breakup of Gondwana and	30-50°S		Continental shelf formed as Indian Ocean opened progressively from	K10	SCP8: Belford 1961 SCP8-5: Belford 1958* SCP8-3: Edgell 1957; Haig <i>et al.</i> 2004* SCP7: Howchin 1907: Chapman 1917; Belford 1960, 1983 SCP7-2: Dixon <i>et al.</i> 2003a*,b*
	SIC SIC	opening of Indian and Atlantic oceans			North to South (~165 Ma in Timor region; ~155 Ma	J50	SCP6-5: Howe <i>et al.</i> 2000 E Cret : Crespin 1963; Jones & Wonders 1992; Haig 1992; Stillwell <i>et al.</i> 2012 SCPA: Edgel 49636, 1963b, Hoje et al. 1006
	LATE JURASSIC				off the Pilbara; ~136 Ma off Perth. Initial marine deposits	J40	SCP4: Edgell 1963a, 1963b; Haig <i>et al.</i> 1996 SCP3: Haig 2005 SCP2: Taylor & Haig 2001 Radiolaria (planktonic)
164	R.E				on shelf were deltaic sands	J30	Pal: Blome 1992 SPC3: Ellis 1993
174	JUR.						

notably prevalent, as evidenced by the prominence of *Ctenidodinium*, *Dissiliodinium*, *Durotrigia* and *Wanaea* types in the *D. caddaense* to *W. indotata* zones of the North West Shelf (Helby *et al.* 1987; Riding *et al.* 2010; Mantle and Riding 2012).

As the opening of the Indian Ocean progressed southward to the Exmouth Plateau region, the Late Jurassic saw a further major period of dinoflagellate cyst diversification, within the now established key tabulation patterns. The abundant experimentation and appearance of short-lived new taxa (Deflandre & Cookson 1955; Cookson & Eisenack 1958; Cookson & Eisenack 1960b; Stover & Helby 1987b) during this epoch has allowed an extremely fine-scale stratigraphic subdivision of the Oxfordian *Wanaea spectabilis* Zone to Tithonian *P. iehiense* Zone (part of), equating to subzones of average duration of less than 500,000 years across the North West Shelf basins.

As the break-up of Gondwana progressed to the Perth Basin margin of Australia, and India rifted off in the Early Cretaceous, progressively more marine conditions developed in the Southern Carnarvon and Perth basins. Backhouse (1987, 1988) neatly documented this succession from the Late Jurassic spore and pollen sequences (Retitriletes watherooensis and Aequitriradites acusus zones) to the marginal and restricted marine, low dinoflagellate diversity assemblages in the Berriasian and most of the Valanginian (Fusiformacysta tumida and Gagiella mutabilis zones) prior to the development of diverse, fully marine assemblages in the latest Valanginian (Kaiwaradinium scrutillinum Zone) and younger stages. These abundant and diverse dinoflagellate cyst assemblages also dominated most North West Shelf assemblages during the Early Cretaceous (Cookson & Eisenack 1958; Stevens 1987; Stevens & Helby 1987; Stover & Helby 1987a, c, d) after moderately restricted dinocyst abundances and diversities in the early Berriasian. The first Australian ceratioids appeared in the latest Tithonian (Pseudoceratium australiense and P. iehiense), whilst the more iconic ceratioid genera, Phoberocysta and Muderongia, arose to prominence in the Hauterivian to Aptian on the North West Shelf (Helby 1987b) and represent some of the most important Early Cretaceous zonal markers.

Dinoflagellate diversity continued to be high in the Valanginian to Cenomanian marine sequences in the post-breakup basins on the west coast as sea-floor spreading progressed and fully marine deposition developed. By the Barremian marine microplankton are also present in parts of the Eucla and Officer basins (Cookson & Eisenack 1970, 1971; Kemp 1976) along the southern margin of Western Australia. A peak of abundance and diversity is reached in the extensive post-breakup Muderong Shale and upper Leederville Formation of the Carnarvon and Perth basins respectively, in the extensively documented *Muderongia australis* Zone, where several new species, including the first *Ovoidinium* species, appear.

The diverse Late Aptian palynofloras have been little studied with only a small number of dinoflagellates formally described from this age (Eisenack & Cookson 1960; Riding & Helby 2001h). By comparison, Albian and Cenomanian dinoflagellate floras are rich and relatively well documented in the Perth and Carnarvon basins (Deflandre & Cookson 1955; Cookson & Eisenack 1958, 1962b, 1969; Eisenack & Cookson 1960) and are dominated by *Diconodinium* and *Spiniferites* lineages (Backhouse 2006).

As a result of a dinoflagellate species turnover near the end of the Cenomanian, few Albian–Cenomanian dinoflagellate species extend into the Turonian and younger strata. *Diconodinium* type cysts disappear, but *Spiniferites* spp. continue to be common and cavate cysts become prominent at many levels (as outlined in an unpublished 1984 University of Western Australia PhD Thesis by N. Marshall). Although well preserved, diverse and abundant, an absence of commercial imperative has resulted in few studies of Late Cretaceous dinoflagellates in Western Australia.

Cenozoic dinoflagellates are known from several formations along the west coast, including the Paleocene– Eocene (Cookson & Eisenack 1961) and the Pliocene– Pleistocene. At species level there is some similarity to south-eastern Australian assemblages and at generic level they are comparable to northern hemisphere dinoflagellates but have not been studied in detail.

Benthic calcareous macroalgae

Shallow-water limestone successions of the warm intervals (viz. Late Devonian-Mississippian, Middle to Late Triassic, Eocene and Early to Middle Miocene) contain diverse calcareous macroalgal assemblages important for evaluation of global biogeography in tropical-subtropical carbonate-platform facies. However, these have been only partly documented and, as shown by the work of Vachard et al. (2014), many recorded taxa require revision. Microfacies have been poorly described and the facies associations are incompletely known. The Mississippian assemblages from the Bonaparte Basin described by Mamet & Roux (1983) lived under normalmarine salinity as indicated by the accompanying diverse invertebrate assemblages including corals (Playford et al. 1975) whereas those from the Southern Carnarvon Basin recorded by Vachard et al. (2014) are associated with a low diversity invertebrate fauna and lived mainly under metahaline conditions.

The recognition of *Tubiphytes* (Fig. 3D, E) by Haig *et al.* (2014) in the lower part of the Callytharra Formation (upper Sakmarian) in the Southern Carnarvon Basin, was significant in changing views of Early Permian climate in Western Australia. The Callytharra Formation represents a southern area of carbonate deposition in the East Gondwana interior rift system that about 2000 km to the north included the type Maubisse Limestone of Timor, also containing *Tubiphytes* (Haig *et al.* 2014). *Tubiphytes* is also present in rare thin limestone beds in the latest Artinksian–earliest Kungurian part of the Noonkanbah Formation of the Canning Basin (Haig *et al.* 2017).

Calcareous nannoplankton

The earliest true calcareous nannoplankton (i.e. those that form heterococcoliths) first appear at the base of the Rhaetian and have an excellent record in the offshore Northern Carnarvon Basin (undocumented, but recorded in unpublished data from exploration wells), and on the Exmouth and Wombat Plateaus (Bralower *et al.* 1991, 1992). The offshore marine Brigadier Formation has abundant and well preserved nannofossils (*Eoconusphaera*, *Crucirhabdus* and *Archaeozygodiscus*), nannoliths (*Prinsiosphaera*) and calcispheres (*Obliquipithonella*, *Orthopithonella* and *Thoracosphaera*). Thick Early Jurassic marine successions in the sub-basins of the Northern Carnarvon Basin contain abundant nannofossils and calcispheres (Howe 2000; Shafik 1993). The nannofossil zonation in this interval has much greater resolution that the spore/pollen zones commonly used in exploration.

Middle Jurassic nannofossils are recorded in the offshore Northern Carnarvon Basin by Howe (2000) and Shafik (1993, 1994). Further south, calcareous nannofossils of this age are known only from the Bajocian assemblages recorded by Shafik (1994) in the Newmarracarra Limestone near Geraldton. Only poor nannofossil assemblages are known from the marine Late Jurassic (Howe 2000), which is puzzling as environments in this interval are mainly offshore marine over the North West Shelf. It is likely related to somewhat restricted surface-water circulation before and immediately after continental breakup in the region.

Throughout most of the Lower Cretaceous, nannofossils are consistently present, but not common. After final continental breakup in the Perth Basin region during the Valanginian, with widespread marine flooding across the Perth and Carnarvon basins, nannofossil abundance and diversity increases markedly from the latest Aptian into the transition from siliciclastic to calcareous sediments in the Turonian-Coniacian. Rich and well-preserved nannofossil assemblages from the Albian-Turonian shales and marls, and the Coniacian-Maastrichtian marls and calcilutites of the western Australian margin were described by Pospichal & Bralower (1992), Moran (1992), Bralower & Siesser (1992), Shafik (1978b, 1990, 1991, 1994), Haig et al. (1996, 2004), Howe et al. (2000, 2003), Campbell et al. (2004), Howe (2005) and Thibault et al. (2012).

There has been little published work on the nannofossil assemblages of the Cenozoic, largely due to the focus of the hydrocarbon exploration industry on the Mesozoic. Shafik (1985, 1978a, c, 1991), Moran (1992), Siesser & Bralower (1992) and Siesser *et al.* (1992a, b) describe Cenozoic nannofossils from Western Australia and relate the assemblages to cosmopolitan stratigraphic zonations.

Foraminifera

During the Late Devonian and Early Carboniferous (Mississippian) there was substantial diversification among Foraminifera world-wide with calcareous Fusulinata rapidly evolving and including a wide variety of chamber shapes, coiling modes, and wall microstructures, particularly during the Mississippian (e.g. Fig. 4A–F). The Western Australian shallow-water limestone formations in the northern basins record this evolution and are significant because they contain the only documented Australian Southern Hemisphere faunas that allow comparison to better known Asian, European and North American assemblages. Fusulinata families that have been described include parathuramminids, pseudoammodiscids,

palaeospiroplectamminids, haplophragminids, koktjubinids, nodosinellids, tournayellids, endothyrids and ozawainellids (Belford 1970; Edgell 2004; Vachard et al. 2014). Some of these provide an important link to the evolution of carbonate-cemented agglutinated Foraminifera, an important benthic foraminiferal group in modern open-shelf seas. Because of the rapid cooling and depositional hiatus during the Pennsylvanian, the foraminiferal succession in Western Australia does not include the evolution of complex fusulinids. The discovery in Timor toward the northern end of the East Gondwana interior rift of a late Gzhelian (latest Pennsylvanian) coral-Tubiphytes reef containing a diverse fusulinid assemblage allowed recognition of a global warm spike, of uncertain cause, that was responsible for the melting of the continental ice sheet covering much of Western Australia (Davydov et al. 2013, 2014).

The importance of the Permian record lies in the evolution of very conservative groups of Foraminifera in the shallow-marine marginal-rift basins that were inundated by restricted seas with estuarine water quality (Haig 2004). The Western Australian basins provide some of the best Permian records of these groups. The organiccemented siliceous agglutinated Foraminifera resemble assemblages from similar facies in the Carboniferous mid-continental basin of North America (Crespin 1958; Haig 2003, 2018; Haig & Mory 2016). A major change in the Nodosariata took place during the late Artinskian (Early Permian) with the appearance of different genera with radiate apertures including the first appearances of Nodosaria, Pyramidulina, Pseudonodosaria and Dentalina that persist to the present-day (Crespin 1958; Haig et al. 2017).

In the warm-temperate Permian intervals when carbonate deposits accumulated in the shallow seas, Foraminifera of Tethyan (warm-water) affinities were present as far south as the Perth Basin. These include lasiodiscids recognized in the Late Sakmarian and late Wordian–Capitanian intervals; endothyrids from the Late Sakmarian and late Wordian–Capitanian; tetrataxids from the Late Sakmarian; abadehellids from the late Wordian– Capitanian (e.g. Fig. 4H, I); and robuloidids from the Wuchiapingian (Crespin 1958; Dixon & Haig 2004; Haig *et al.* 2014; and unpublished data).

Although the Triassic and Jurassic foraminiferal faunas from mudstone facies are poorly documented, the excellent preservation of assemblages recorded by Heath & Apthorpe (1986, Triassic), Apthorpe (2003, Triassic) and Bartenstein & Malz (2001, Middle Jurassic) indicate that when the faunas are better known they will provide significant information particularly about the evolution of the Triassic duostominids and the aragonitic Jurassic ceratobuliminids and epistominids.

The shelf basins of the Cretaceous contain an almost complete Cretaceous marine section. The succession on the Southern Carnarvon Platform with mudstone facies ranging from the Barremian to Cenomanian followed by chalk facies from the Turonian to Maastrichtian provides a standard outcrop reference section for placing the Australian Cretaceous in a global context. Continuous stratigraphic cores in selected boreholes complement the outcrop sections and enable benthic and planktonic foraminiferal successions to be related to zones based on calcareous nannoplankton, dinoflagellates and other palynomorphs (Dixon et al. 2003a,b; Haig *et al.* 2004). The Lower Cretaceous mudstone succession includes foraminiferal assemblages of estuarine aspect similar to those found in the marginal rift basins of the Western Australian Permian (Haig 2004). The Late Cretaceous planktonic foraminiferal succession from chalk facies, described from subsurface cored sections on Exmouth Plateau and the North West Shelf, forms the basis of an Indian Ocean mid-latitude zonation and provides important oceanographic indicators in the juvenile Indian Ocean (Petrizzo 2000, 2003; Petrizzo & Premoli Silva 2000; Howe *et al.* 2003; Campbell *et al.* 2004).

Western Australian Cenozoic foraminiferal faunas have been incompletely documented (see references listed on Table 5). The Paleocene–Eocene and Lower to Middle Miocene carbonate successions, outcropping in the Giralia and Cape Range Anticlines between Carnarvon and Exmouth may provide a standard midlatitude faunal record for the Indian Ocean region when the faunas are better known.

Radiolaria

Fossil radiolarian assemblages are generally found in radiolarian ooze deposited on the deep ocean floor. The ooze is often preserved in orogenic outcrop belts as radiolarian chert or siliceous argillite; see, for example, the Middle Jurassic siliceous argillite with a diverse radiolarian assemblage described from Timor by Haig & Bandini (2013) and used as evidence for continental breakup and the opening of the Indian Ocean in the Timor region during the late Bathonian–early Callovian.

In contrast to radiolarians from deep-sea chert, in Western Australia diverse radiolarian assemblages have been described from Late Devonian shallowwater interior-sea mudstone facies of the Canning Basin (Nazarov et al. 1982; Nazarov & Ormiston 1983; Aitchison 1993; Won 1997a, 1997b) and Early Cretaceous restricted marginal shelf mudstone deposits of the Southern Carnarvon Platform (Ellis 1993). These are therefore of considerable interest because of the facies contrast with the deep-ocean deposits. Haig (2005) showed that the Windalia Radiolarite, from the Aptian (Early Cretaceous) of the Southern Carnarvon Platform, was a radiolarian-rich mudstone deposited in the mid-neritic zone, and that radiolarians formed part of the plankton in the epicontinental seas at shallower water depths than preferred by planktonic foraminifera. This view is supported by the coeval radiolarian assemblages known from the Surat Basin of Queensland, part of the area flooded in the interior of Australia during the Barremian to Albian (Haig & Barnbaum 1978).

FOCUS FOR FUTURE STUDIES

In publications, only a small fraction of species of most of the groups discussed in this paper have been systematically described and evaluated using modern observational methods and up-to-date taxonomy. Because of this, consistent recognition by different workers of the biostratigraphic ranges of the species is difficult to establish, as is integration of biozonations based on the different groups. If this could be achieved, finer-scale correlation and environmental interpretations may be possible within the sedimentary basins, and a clearer pattern of evolution and/or migration of species could be established.

Among the organic-walled phytoplankton a major gap appears in published records of acritarchs from the Silurian of Western Australia. This is clearly an area for further investigation and is best explored in the subsurface Silurian strata of the Southern Carnarvon Basin where acritarchs have been reported in petroleum industry reports. Among dinoflagellates, more detailed documentation of species assemblages and the environmental controls on these is required throughout the Mesozoic and also in the very poorly understood Cenozoic record.

The Late Triassic, Paleogene (Middle Eocene) and Neogene (Early to Middle Miocene) contain diverse macroalgal assemblages that have not been described. The systematic evaluation of these assemblages will be important in biogeographic comparisons particularly with coeval assemblages in exotic terranes emplaced during the tectonic collisions on the northern and northwestern margins of the continent.

Among the calcareous nannoplankton, the Late Triassic, Jurassic and Early Cretaceous assemblages have not been fully documented. Systematic documentation of these assemblages will assist greatly in calibrating the ages of the dinoflagellate and spore/pollen zonations that are so important for hydrocarbon exploration. Because of the focus of the hydrocarbon exploration industry on the Mesozoic, Cenozoic nannofossils from Western Australia have received little attention. Further study of this interval should yield improvements in biostratigraphic resolution and also provide greater palaeo-oceanographic information concerning the eastern Indian Ocean during the Paleogene and Neogene.

Large gaps in the published fossil record of Western Australian Foraminifera are present in the Mississippian shale successions of the Bonaparte Basin, the marine Triassic–Jurassic successions of the North West Shelf, and the Cretaceous–Paleogene strata of the continental shelf basins, including those along the southern margin. Better knowledge of these microfaunas may lead to a greater understanding of foraminiferal evolution and migration both within interior basins and on a continental shelf transgressing latitudes and climatic belts through time.

The Early Cretaceous (late Aptian) radiolarian fauna from the Windalia Radiolarite has only been described from the type outcrop section of this formation. Equivalent Early Cretaceous radiolarian-rich mudstone successions are widespread in Western Australian basins and are known in Cretaceous basins across Australia. The distribution of radiolarians species within these rocks may lead to a better understanding of water-quality conditions associated with the major Early Cretaceous marine transgression across the continent.

CONCLUSIONS

(1) Algae and testate protozoans form an important component of the Western Australian Phanerozoic fossil record. Representatives of these groups, particularly the acritarchs, dinoflagellates, calcareous nannofossils and foraminifera are important stratigraphic guides in petroleum and groundwater exploration and much unpublished industry work has been done on these microfossils.

(2) Changes in continental configuration, palaeolatitudes, climate and marine inundations that affected Western Australian basins during the Phanerozoic are reflected in the stratigraphic record of algae and testate protozoans.

(3) The Paleozoic and early to mid-Mesozoic fossil assemblages are from shallow interior seas of East Gondwana that varied from a warm Northern Hemisphere position during the Ordovician to high latitudes during the Pennsylvanian when the region was covered by a continental ice sheet, followed by variable humid climatic conditions during the Permian and generally warm to temperate humid conditions during the Triassic and Jurassic.

(4) Open continental shelves and marginal continental plateaus facing the Indian Ocean developed first in northern Western Australia during the Middle Jurassic, with continental breakup and ocean formation progressively taking place in segments toward the South (Late Jurassic in the Argo Abyssal Plain, north of Exmouth Plateau; Early Cretaceous in the Perth Abyssal Plain). The opening of the Indian Ocean and the almost concomitant opening of the Atlantic Ocean led to major changes in ocean-circulation patterns. These changes probably allowed a marked diversification of dinoflagellates and foraminifera (particularly planktonic types) during the Late Jurassic and Cretaceous, and resulted in assemblages that even by the latest Cretaceous began to resemble the modern biota of the Western Australian continental margin.

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